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# The Functional Role of Leaf Nutrients in an Old-Field Successional Community

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The Functional Role of Leaf Nutrients in an Old-Field Successional Community

BY

Kirstin I. Duffin

**THESIS**

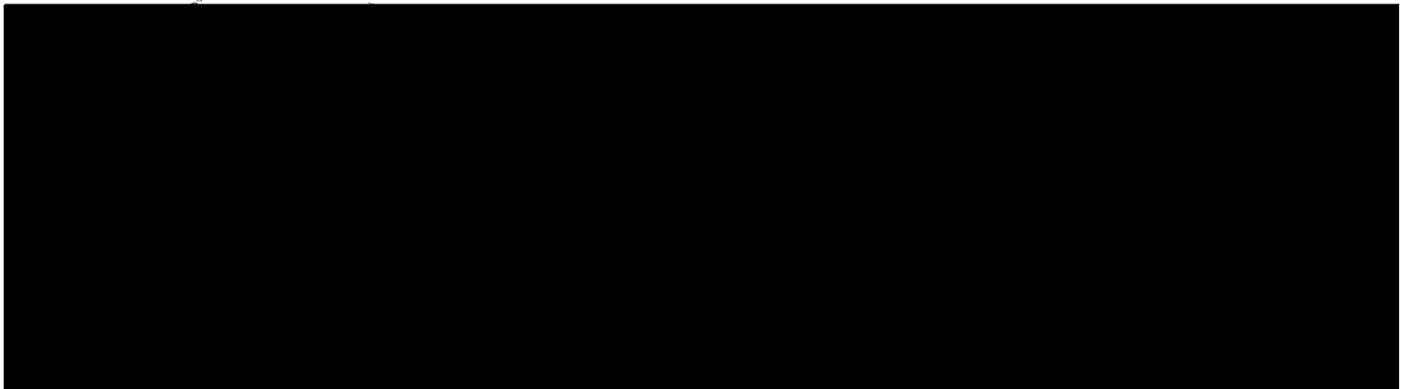
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FOR THE DEGREE OF

Master of Science in Biological Sciences

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY  
CHARLESTON, ILLINOIS

2015

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## **Abstract**

In functional ecology, traits that capture aspects of plant performance are used to understand how organisms interact with their environment. Leaf nutrients are an example of a functional trait that directly links to plant metabolic processes and therefore may describe plant assemblage dynamics. Multivariate leaf nutrient analyses may be used with other functional traits to understand ecological strategies because they are a direct measure of leaf metabolic processes and can describe nuances in plant allocation patterns. In this thesis, I explored (1) whether a suite of leaf nutrients (carbon, nitrogen, phosphorus, potassium, calcium, and magnesium) was related to plant growth form (forb, graminoid, or woody plant), species origin (native or exotic), or invasiveness (invasive or non-invasive), (2) how these nutrients were associated across species and whether these relationships were different among species' groups, and (3) how leaf nutrients related to Westoby's leaf-height-seed (LHS) scheme and to a successional gradient.

Healthy, mature leaves were taken from 122 species across a wide range of growth forms in a mesic continental community of successional fields and young and old-growth oak-hickory forests in New Jersey, USA. Multivariate analyses of leaf nutrients by growth form, origin, and invasiveness were conducted, as well as correlations of leaf nutrients by growth form and with specific leaf area (SLA), maximum height, seed mass, and peak successional year. The primary factor in variation of leaf nutrient patterns was growth form. Forbs had the strongest nutrient associations and had greater levels of leaf macronutrients compared with woody and graminoid species, which had higher amounts of foliar carbon. After distinguishing leaf nutrient allocation strategy by growth form, there were minimal relationships between leaf nutrients and plant origin

and invasiveness. SLA and seed mass, but not height or peak successional year, were correlated with leaf nutrients of some growth forms.

In community level studies, comparisons should be made by plant growth form or analyses will yield spurious results. While the focus of the literature thus far has been on carbon and nitrogen, understanding the relationships with other leaf nutrients will help describe the nuances of tradeoffs in plant growth strategies. This understanding will inform restoration ecology of successional communities.

## **Dedication**

To Dad, a man whose intelligence and pensiveness have motivated me and whose embodiment of encouragement and kindness have inspired me.

To Mom, whose spunk warms me and whose love and care have allowed me to succeed.

You both have instilled in me the curiosity to explore.

and

To Clyde. You endured my moments of fret and gently brought me to a place of achievability. Thank you for your infinite patience and support.

## **Acknowledgments**

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Much appreciation is due to Dr. Thomas Canam and Dr. Barbara Carlsward. Thank you for serving on my committee and providing thoughtful feedback to my work.

Many people have served as data collectors for the Buell-Small Succession Study over the years. Their labor has allowed me to ask the questions I did for this thesis.

Thank you to Ellen Corrigan and Dr. John Stimac for lending non-biological expertise to revisions of this thesis. Your comments were especially helpful in working through a final review.

My library colleagues have given me support and space to accomplish my master's work. I could not have asked to work with a finer group of people.

and

Thanks to Leon Mire. Your engaging questions prompted in me renewed interest to pursue this project. Your keen insights helped me to see the bigger picture and to refine and strengthen my writing. Your friendship is treasured.

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## **Introduction**

One of the major innovations in community ecology has been a shift toward a focus on functional ecology. In functional ecology, suites of traits rather than species' taxonomic identities are used to describe relationships between organisms at the community and ecosystem levels (Keddy 1992, Duarte et al. 1995). A set of core functional traits (e.g., canopy height, seed mass, specific leaf area, woodiness) are used to capture how plants acquire and use resources (Diaz et al. 2004). Traits correspond to environmental conditions in which a given group of plants grows and are identifiable across species, making traits more universally descriptive of plant distributions than taxonomic affinity (Keddy 1992). Understanding how functional traits are predictive of organism-level resource allocation allows for modeling of these patterns to describe the dynamics of assemblages at larger scales (Irschick et al. 2013).

As functional traits, leaf nutrient concentrations reflect both the physical and physiological function of leaves and thereby may help to explain plant assemblage dynamics. Nitrogen, a major limiting nutrient to plant growth yet needed in large amounts, has been a focus of many studies. Leaf N levels, in part, establish a plant's photosynthetic capacity (Field and Mooney 1986, Evans 1989, Wright et al. 2004), though this relationship is influenced by leaf P levels (Reich et al. 2009). Leaf N is not only related to the physiological activity of a species but also to characteristics important to community and ecosystem processes. High leaf N is positively correlated with greater seed mass (Laughlin et al. 2010), a critical determinant of establishment success and dispersal in plants (Westoby et al. 1996). Higher leaf C:N and C:P and lower N:P ratios decrease leaf palatability to herbivores (Kurokawa et al. 2010), altering the flow of

nutrients through ecosystems. The importance of leaf N and other nutrients to species' performance indicates that leaf nutrients are fundamental functional traits.

As fundamental measures of leaf function, the composition of nutrient elements in leaves may reflect plant growth form, origin, and invasiveness. Leaf nutrients are related to plant growth form across a wide range of habitats (e.g., Bigelow 1993; Foulds 1993; Thompson et al. 1997; Han et al. 2005; Bombonato et al. 2010). Leaves of herbaceous plants (forbs and graminoids) tend to have higher levels of macronutrients than woody plants (Foulds 1993, Han et al. 2005), and forbs tend to have the highest concentrations of leaf macronutrients as compared to graminoid and woody species (Bombonato et al. 2010). Depending on the nature of the study, it may be important to distinguish plant origin (native or exotic) from invasiveness (invasive or not) to compare functionally equivalent species and ensure appropriateness of comparisons (van Kleunen et al. 2010a, 2010b). Some evidence shows that exotic plants have higher foliar nutrient content of some elements than native plants (Foulds 1993, Osman and Sikder 2000). Invasive and non-invasive plants grown under greenhouse conditions have been shown not to differ significantly in leaf N composition (Matzek 2011), although invasive species growing in a botanical garden had lower leaf N than non-invasive species (Feng et al. 2008). Invasive species tend to have greater leaf nutrient concentrations for some elements as compared to native plants across forb and woody species (Drenovsky et al. 2008, Peñuelas et al. 2010), although the opposite has been documented in tree seedlings (Lamarque et al. 2013). Plant growth form, origin, and invasiveness may independently affect leaf nutrient levels, and there may be interactive effects of these groupings on foliar nutrient levels.

Nutrient availability to plants varies depending on the successional age of the community, leading to altered nutrient use patterns in species of differing successional stages. In general, later successional communities have more closed nutrient cycles (Odum 1969, Bazzaz 1979). During secondary succession, plant communities shift from early annual and perennial forb dominance to shrub and tree dominance in later successional stages. Shifts in foliar nutrient allocation patterns should reflect the successional shifts in community structure associated with changes in plant growth form. Community composition shapes litter and decomposition rates and therefore soil nutrient availability (e.g., Mitchell et al. 1997; Ehrenfeld et al. 2001; Berg and Laskowski 2006).

To fully understand the functional linkages of leaf nutrient concentrations in plant communities, broad scale surveys of leaf nutrients in dynamic plant communities are necessary. This study analyzed the leaf nutrient composition of a broad suite of plants growing in a temperate system undergoing succession from agricultural fields to deciduous forest to address the following questions: 1) Are leaf nutrient concentrations functionally associated with plant growth form, origin, or invasiveness? 2) What are the associations among leaf nutrients and do these patterns vary among species' groups? 3) How is leaf nutrient stoichiometry related to other plant functional traits and to species' successional roles?

## Methods

### *Site*

The Buell-Small Succession Study (BSS) is a long-term research project documenting successional vegetation changes from abandoned agricultural fields to a deciduous forest community. The BSS fields are located in what is now the Hutcheson Memorial Forest Center (HMFC) in the Piedmont region of Somerset County, New Jersey (40°30' N, 74°34' W, Fig. 1). Climatic conditions are mesic continental. Mean annual temperature is 11.5°C, ranging from an average high of -1.2°C in January to 23.7°C in July. Mean annual precipitation is 1,180 mm, averaging 76 mm in February and 123 mm in July (New Jersey State Climatologist; National Climate Data Center). Soil in the HMFC is derived from Triassic red shale of the Brunswick Formation (Kümmel 1940; Ugolini 1964).

The HMFC is a mosaic of deciduous old-growth forest, young forest, and successional fields. The old-growth forest of the site is a mixed *Quercus-Carya* canopy with a subcanopy of *Cornus florida* and shrub layer dominated by *Viburnum acerifolium* (Monk 1961, Davison and Forman 1982). This forest is surrounded by the fields of the BSS as well as other areas in various successional stages, including agricultural land. This landscape is thus a heterogeneous mixture of communities representing all successional stages within a small area.

The BSS contains ten hay and row crop fields, 0.5-1 hectare each, that were abandoned in pairs following either crop harvest (intact litter) or one final plowing (bare soil) from 1958 to 1964. Vegetation dynamics in each of these fields have been monitored with no intervention in a series of 48 permanent plots, 1 m<sup>2</sup> each. Plots were

censused annually from 1958 to 1979 and biennially thereafter, recording percent cover of all species growing in each plot. Data from the BSS provide the linkage to community successional dynamics for my leaf nutrient survey.

### *Sampling and plant trait analysis*

Healthy, mature leaves were collected from 122 species across the HMFC in late July over a three-year period, with most specimens gathered in 2010. Samples represented 48 families and 94 genera, and included 75 native and 44 exotic species (Appendix). Species collected were chosen to represent successional dominants throughout the BSS, species characteristic of mature forests, and species currently expanding in the site. Samples were taken from healthy mature individuals growing under optimal environmental conditions. When available, leaves from ten or more plants were collected and treated as one sample to give a single species value. For small herbaceous plants, samples were often taken from 20 or more individuals to collect sufficient tissue for chemical analyses. Leaves were dried at 60°C for 48 hours and stored dry until processed. Samples were sent to the University of Georgia Stable Isotope Lab (Athens, GA) to analyze leaf nutrient levels. Leaf C and N were analyzed using Micro-Dumas combustion. Leaf P values were obtained through continuous flow colorimetric analysis. Leaf K, Ca, and Mg were analyzed by flame atomic absorption spectrophotometry.

Other plant trait data were collected following the guidelines from Cornelissen et al. (2003) from the HMFC and surrounding areas when necessary as part of the larger BSS project. Functional traits were selected following Westoby's (1998) leaf-height-seed

scheme. Specific leaf area (SLA) was collected in the field as part of the BSS database during earlier studies. Plant height data were assembled from Gleason and Cronquist (1991) and Mohlenbrock (2002) and supplemented with field measurements when necessary. Seed mass data were gathered from published sources and supplemented with field measurements.

Literature sources were used to classify species into native/exotic and invasive/noninvasive categories. Plant invasiveness was considered separately from origin in analyses according to recommendations by van Kleunen et al. (2010a). Of the species sampled, 45 were considered invasive within and outside the United States, while 74 were non-invasive (Boršić et al. 2008; Lambdon et al. 2008; Weber et al. 2008; Pyšek et al. 2012; Ries et al. 2013; USDA NRCS n.d.). A total of 62 non-invasive native, 13 invasive native, 12 non-invasive exotic, and 32 invasive exotic species were analyzed. Origin and invasiveness data for *Carex* sp., *Juncus* sp., and *Viola* sp. were not listed, as these samples were identified only to the genus level. Samples included 17 annual, 13 biennial, 46 perennial, 14 shrub, 6 liana, and 23 tree species (Table 1). Nomenclature follows the USDA NRCS PLANTS Database (<http://plants.usda.gov>) as of June 2014.

### *Statistical analyses*

Nutrient data were log transformed prior to all statistical analyses. To understand the relationships between leaf nutrient stoichiometry and plant form, origin, and invasiveness, nutrient data were analyzed by growth form (forb, graminoid, woody) and origin (native, exotic) or invasiveness (invasive, non-invasive), with interaction effects in two-way MANOVAs followed by univariate ANOVAs. Tukey's HSD post hoc tests

were used to indicate where significant relationships occurred in growth form analyses. Patterns of leaf nutrient associations within forb and woody growth forms were assessed using Pearson correlation coefficients followed by Bonferroni correction for multiple comparisons.

To visualize multivariate relationships within the data, a principal components analysis (PCA) was conducted on all leaf nutrients using a correlation matrix. PCA coordinates from the first two axes were plotted to show form  $\times$  origin and form  $\times$  invasiveness effects. PCA scores were also used to determine associations of leaf nutrient chemistry with successional status and other plant traits using Pearson correlations followed by Bonferroni correction. Peak successional year was determined from the BSS data by evaluating when each species reached its greatest percent cover, averaged across all 10 fields.

All statistical analyses were conducted using SAS version 9.2 (SAS Institute Inc., Cary, North Carolina, USA).

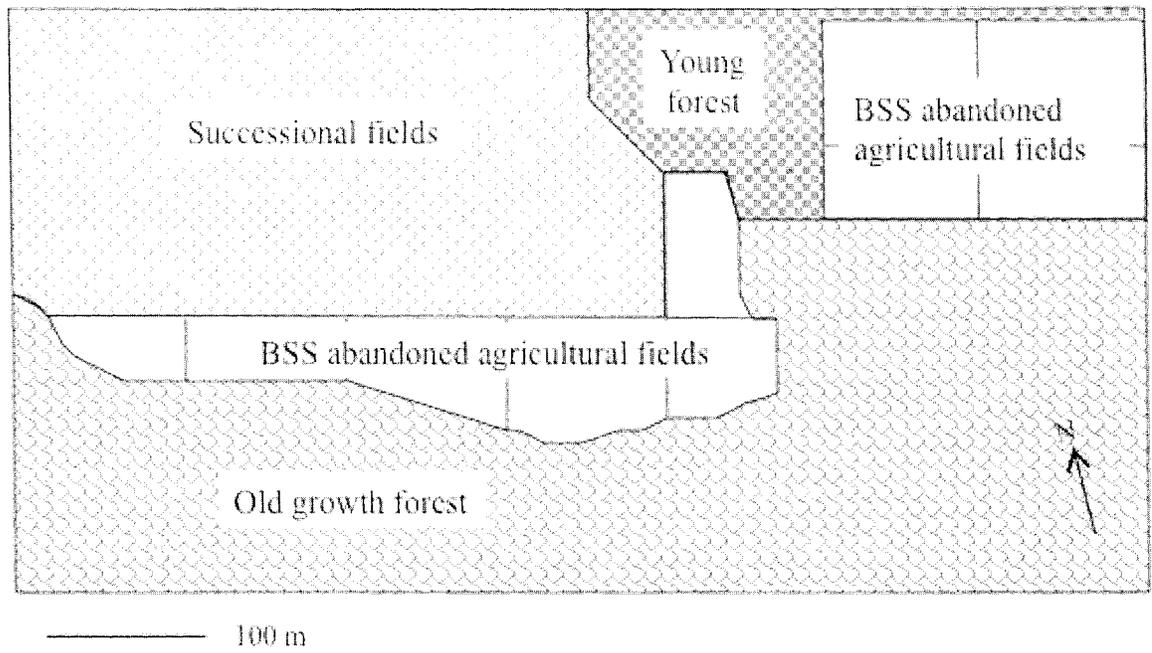


Figure 1. Map of study site. Abandoned agricultural fields comprise the Buell-Small Succession Study (BSS).

Table 1. Number of species sampled by growth form, origin, and invasiveness.

Growth Form		Native	Exotic	Invasive	Non-Invasive
Forb	Annual	9	4	6	7
	Biennial	3	10	6	7
	Perennial	30	9	13	26
Graminoid	Annual	0	4	4	0
	Perennial	3	4	1	6
Woody	Shrub	9	5	5	9
	Liana	3	3	4	2
	Tree	18	5	6	17

## Results

Leaf nutrient stoichiometric patterns were significantly different among plant growth forms but not between origin or invasiveness groupings with no significant interactions (Tables 2 and 3). All individual leaf nutrient concentrations significantly varied among growth forms (Tables 2 and 3). Woody species had higher C than forbs (Fig. 2). Forbs tended to have greater amounts of leaf macronutrients than woody species, although forb and woody species had statistically similar levels of Ca. Graminoid species had moderate levels of C and N compared to forb and woody species. Graminoids were similarly high in P and K as forbs, similarly low in Mg as woody species, and had the lowest Ca levels of all growth forms. While the MANOVA showed no overall effect of species origin on leaf nutrient concentrations, univariate tests found C was significantly higher and K significantly lower in native species (Table 2).

Patterning of leaf nutrients was stronger in forbs, as nutrient concentrations were more frequently correlated than in woody plants (Table 4). Across forb and woody life forms, when correlations were significant, C was negatively correlated with the macronutrients and the macronutrients were positively correlated with one another. In forbs, C was negatively correlated with all foliar mineral nutrients except Ca. Leaf N and P were positively correlated with all macronutrients excluding Ca in forbs. Leaf C in woody species was negatively correlated with K and Mg. In addition, P was positively correlated with N and K, and Ca was positively correlated with Mg among woody plants. Leaf N and P, as well as Ca and Mg, were more strongly correlated among woody species than forbs. Graminoid species were not included in this analysis due to low sample size ( $n = 13$ ).

The PCA generated two informative axes explaining 52 and 22% of the variation in the data, respectively. The mineral nutrients N, P, K, Ca, and Mg correlated positively and C correlated negatively with axis I of the PCA (Fig. 3A). Axis II was positively correlated with Ca and Mg and negatively correlated with N and P. Foliar nutrient stoichiometry differed among growth forms in this analysis (Fig. 3B). Graminoid and woody species tended to load negatively and toward leaf C on axis I, while forb species loaded positively and toward the mineral nutrients. Axis II separated growth forms fairly cleanly with graminoid species loading negatively, forb species around the origin, and woody species loading positively. The forb at the far right of Fig. 3B is *Portulaca oleracea*, which was the only species in the system to have succulent leaves. The graminoid on the lowest portion of both axes is *Juncus* sp., the only rush in this study, which had the lowest N, P, K, Mg, and Ca of this growth form. The graminoid on the lowest portion of PCA axis II, near the origin of PCA axis I, is *Elymus repens*, which had the highest K and among the lowest Ca of the graminoids.

Leaf nutrient patterns by origin and invasiveness were less striking. Native species loaded more negatively on axis I than exotic species for both forb and woody growth forms, but native and exotic species within both growth forms loaded similarly on axis II (Fig. 4A). Non-invasive species exhibited similar patterns to native species, loading more negatively on axis I than invasive species and loading similarly on axis II in both forb and woody forms (Fig. 4B). Graminoid species were excluded from these analyses due to low sample size.

There were limited correlations between foliar nutrient stoichiometry and other plant functional traits. Among growth forms, SLA of forbs was positively correlated with

PCA axis I (Table 5). Seed mass of forbs was positively correlated with PCA axes I and

II. Height was not correlated with leaf nutrient patterns for any growth form.

Successional peak year in abundance was not correlated with foliar nutrient stoichiometry in any growth form.

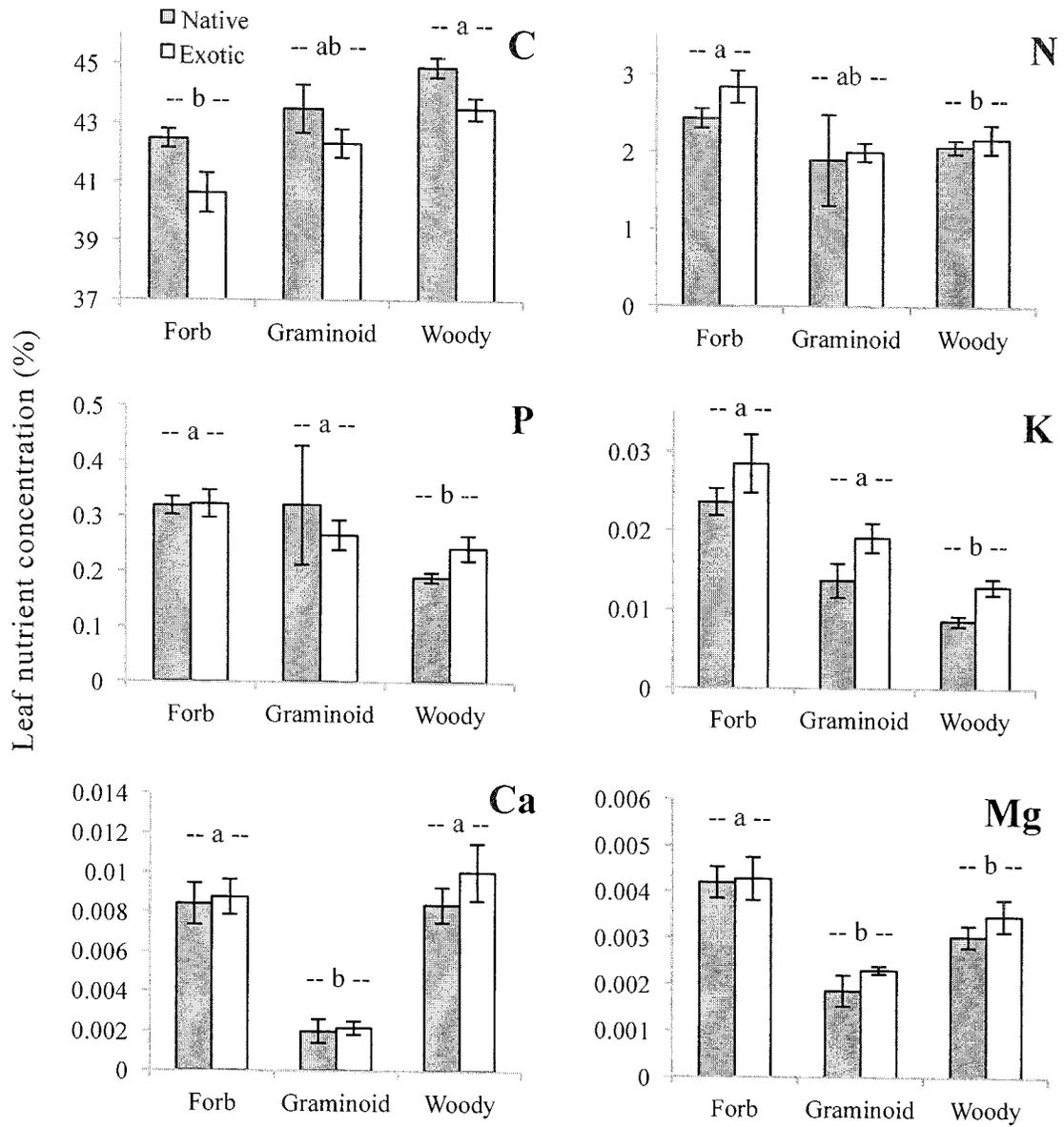


Figure 2. Leaf nutrients by growth form and origin. Bars represent mean  $\pm$  standard error. Dissimilar letters represent significant difference between growth forms. Note varying scales on y-axes between nutrients.

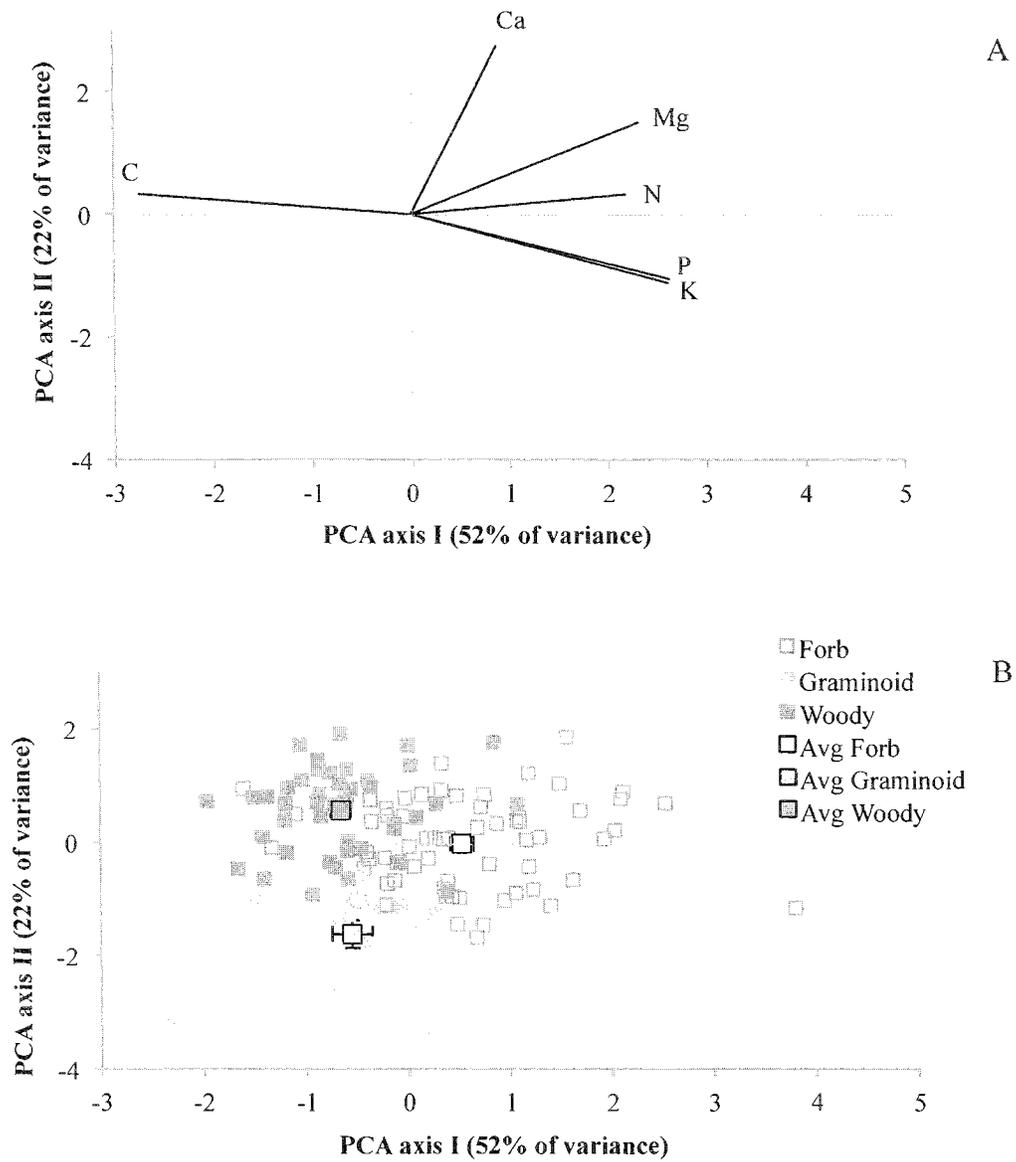


Figure 3. (A) Relationship between leaf nutrients using principal components analysis. (B) Forb (n = 66), graminoid (n = 13), and woody (n = 43) species as they relate to PCA axis I and II. Average values plotted are mean  $\pm$  standard error.

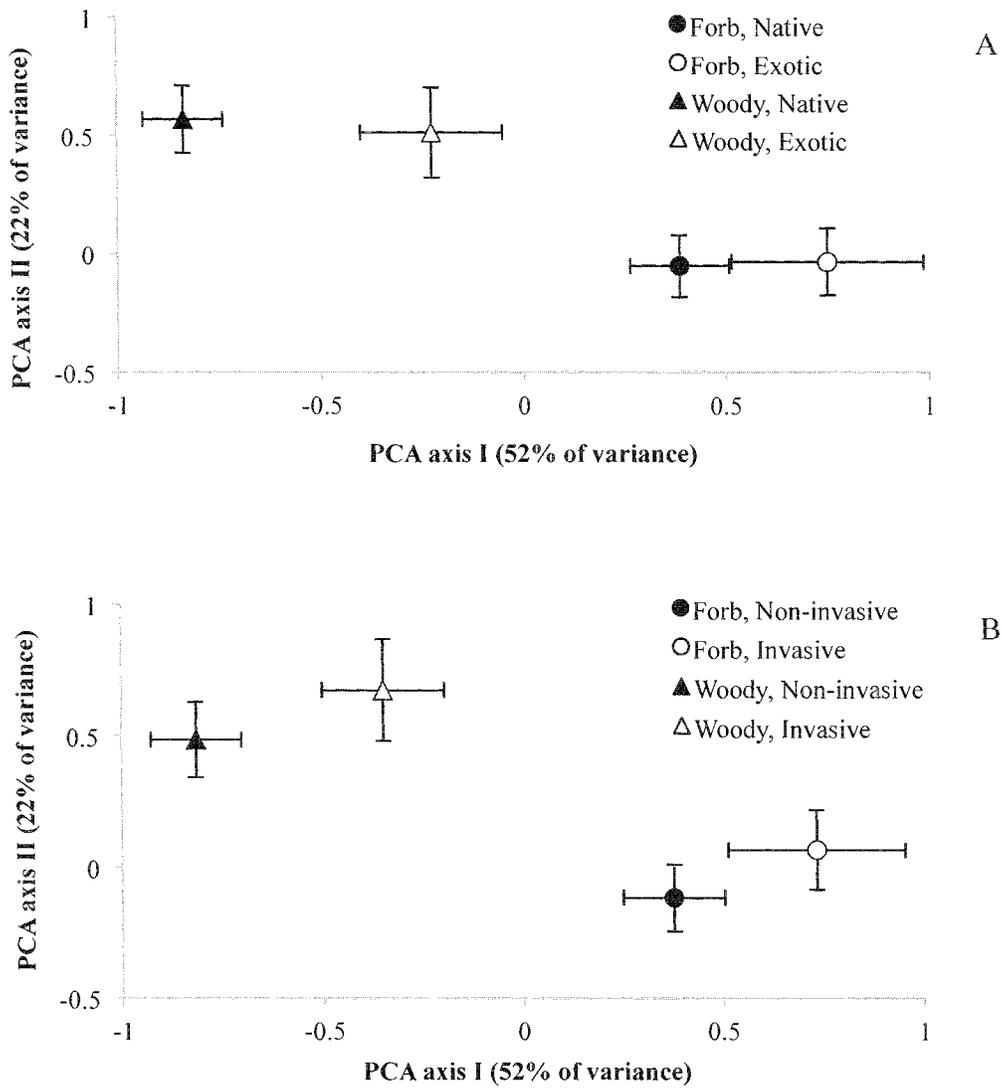


Figure 4. Average values of growth form by (A) origin and (B) invasiveness as they relate to PCA axis I and II. Graminoids were omitted due to low sample size. Values plotted are mean  $\pm$  standard error.

Table 2. Nutrient associations with plant growth form, species origin, and the interaction between form and origin using MANOVA. Significant values ( $p < 0.05$ ) are in bold.

	df	MS/Pillai's Trace	F	p
<b>Multivariate test</b>				
Form	12, 218	0.737	10.60	<b>&lt;0.0001</b>
Origin	6, 108	0.081	1.58	0.1595
Form x Origin	12, 218	0.171	1.70	0.0692
<b>Univariate tests</b>				
<b>C</b>				
Form	2	0.0087	15.57	<b>&lt;0.0001</b>
Origin	1	0.0033	5.83	<b>0.0174</b>
Form x Origin	2	0.0002	0.28	0.7594
error	113	0.0006		
<b>N</b>				
Form	2	0.108	5.73	<b>0.0043</b>
Origin	1	0.026	1.39	0.2412
Form x Origin	2	0.006	0.29	0.7482
error	113	0.019		
<b>P</b>				
Form	2	0.313	17.47	<b>&lt;0.0001</b>
Origin	1	0.005	0.30	0.5877
Form x Origin	2	0.035	1.96	0.1457
error	113	0.018		
<b>K</b>				
Form	2	1.404	35.15	<b>&lt;0.0001</b>
Origin	1	0.240	6.00	<b>0.0159</b>
Form x Origin	2	0.053	1.33	0.2693
error	113	0.040		
<b>Ca</b>				
Form	2	1.523	24.02	<b>&lt;0.0001</b>
Origin	1	0.047	0.74	0.3906
Form x Origin	2	0.012	0.18	0.8320
error	113	0.063		
<b>Mg</b>				
Form	2	0.325	9.18	<b>0.0002</b>
Origin	1	0.054	1.52	0.2206
Form x Origin	2	0.015	0.43	0.6546
error	113	0.035		

Table 3. Nutrient associations with plant growth form, invasiveness, and the interaction between form and invasiveness using MANOVA. Significant values ( $p < 0.05$ ) are in bold.

	df	MS/Pillai's Trace	F	p
<b>Multivariate test</b>				
Form	12, 218	0.829	12.87	<b>&lt;0.0001</b>
Invasiveness	6, 108	0.042	0.80	0.5730
Form x Invasiveness	12, 218	0.118	1.14	0.3270
<b>Univariate tests</b>				
<b>C</b>				
Form	2	0.0094	15.75	<b>&lt;0.0001</b>
Invasiveness	1	0.0023	3.83	0.0529
Form x Invasiveness	2	0.0002	0.25	0.7772
error	113	0.0006		
<b>N</b>				
Form	2	0.101	5.25	<b>0.0066</b>
Invasiveness	1	0.001	0.06	0.8048
Form x Invasiveness	2	0.006	0.32	0.7282
error	113	0.019		
<b>P</b>				
Form	2	0.365	20.23	<b>&lt;0.0001</b>
Invasiveness	1	0.049	2.72	0.1019
Form x Invasiveness	2	0.019	1.08	0.3433
error	113	0.018		
<b>K</b>				
Form	2	1.650	39.15	<b>&lt;0.0001</b>
Invasiveness	1	0.090	2.13	0.1471
Form x Invasiveness	2	0.013	0.30	0.7401
error	113	0.042		
<b>Ca</b>				
Form	2	1.881	30.54	<b>&lt;0.0001</b>
Invasiveness	1	0.011	0.17	0.6779
Form x Invasiveness	2	0.089	1.44	0.2412
error	113	0.062		
<b>Mg</b>				
Form	2	0.358	10.31	<b>&lt;0.0001</b>
Invasiveness	1	0.049	1.42	0.2362
Form x Invasiveness	2	0.005	0.15	0.8646
error	113	0.035		

Table 4. Leaf nutrient correlations by growth form. Forb growth form analysis on top right (n = 66). Woody growth form analysis on bottom left (n = 43). Bonferroni-adjusted significance values to maintain an overall  $\alpha$  of 0.05 for each growth form ( $p < 0.0033$ ) are in bold.

	C	N	P	K	Ca	Mg
<b>C</b>						
r	---	-0.45786	-0.62479	-0.62786	-0.31958	-0.60711
p		<b>0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.0089	<b>&lt;0.0001</b>
<b>N</b>						
r	-0.07769	---	0.38537	0.38640	0.08557	0.40732
p	0.6205		<b>0.0014</b>	<b>0.0014</b>	0.4945	<b>0.0007</b>
<b>P</b>						
r	-0.36177	0.58989	---	0.56387	-0.07983	0.38270
p	0.0171	<b>&lt;0.0001</b>		<b>&lt;0.0001</b>	0.5240	<b>0.0015</b>
<b>K</b>						
r	-0.54267	0.20627	0.59174	---	-0.08763	0.30822
p	<b>0.0002</b>	0.1845	<b>&lt;0.0001</b>		0.4842	0.0118
<b>Ca</b>						
r	-0.31258	-0.10089	-0.07507	0.18824	---	0.31240
p	0.0413	0.5198	0.6323	0.2267		0.0107
<b>Mg</b>						
r	-0.50679	-0.02341	0.15307	0.28286	0.52021	---
p	<b>0.0005</b>	0.8815	0.3271	0.0661	<b>0.0003</b>	

Table 5. Plant traits by growth form correlated to the PCA coordinate data using Pearson correlation coefficient values. Log-transformed data for SLA, seed mass, and height were used for the correlations. Peak year is over 53 years of succession. Bonferroni-adjusted significance values ( $p < 0.0125$ ) are in bold.

Growth form	Trait	Mean	n	PCA Factor 1	PCA Factor 2
Forb	SLA	289.6 cm <sup>2</sup> /g	66	<b>0.3482</b>	0.0407
	Seed mass	1.38 mg	66	<b>0.3982</b>	<b>0.3566</b>
	Height	1.16 m	65	-0.1475	0.0906
	Peak year	14.26	66	0.0577	0.0330
Graminoid	SLA	191.1 cm <sup>2</sup> /g	13	0.4324	0.4575
	Seed mass	1.01 mg	13	-0.3038	-0.1749
	Height	0.92 m	13	0.2657	0.2120
	Peak year	13.85	13	-0.1648	0.1889
Woody	SLA	174.4 cm <sup>2</sup> /g	43	0.1723	0.0592
	Seed mass	502.00 mg	43	-0.4163	-0.1484
	Height	19.30 m	42	-0.1586	-0.0124
	Peak year	33.95	43	-0.2118	-0.2252

## **Discussion**

This survey found a wide range of nutrient levels across the 122 species studied. This is perhaps not surprising, as the study included species from a broad span of growth forms and successional roles. The primary factor was that each plant growth form has unique leaf nutrient profiles. As such, all subsequent analyses of leaf nutrients were partitioned by form in order to make analogous comparisons. This allowed me to determine more subtle patterning and variation of drivers within these diverse groups.

### *Growth form and leaf nutrients*

Leaf nutrient levels in plants varied greatly across growth forms. Forbs had the highest levels of macronutrients relative to carbon. This pattern fits the fast growth rate and short leaf life span of forbs relative to woody plants (Grime and Hunt 1975, Tilman 1988, Reich et al. 1998, Wright et al. 2004). The forb growth strategy requires relatively high nutrient allocation to leaves, especially of N, in order to maximize photosynthesis and, therefore, carbon capture (Chapin 1980). In this way, forbs are able to produce biomass and establish leaf area more quickly than resource-conservative woody plants. This fast growth cycle allows forbs to have the competitive edge over woody species in the short term.

This strategy of resource acquisition within the forbs has long been documented (Foulds 1993, Reich et al. 1998, Peng et al. 2011). However, not all studies have found a strong correlation between leaf nutrients and growth form. Herbs, shrubs, and trees had similar levels of foliar N and P in a temperate deciduous forest (Chen et al. 2011). The contrast with my findings is likely because I separated the herbaceous species into

graminoids and forbs due to their large differences in leaf stoichiometry. Pooling low nutrient concentration graminoids with forbs would make herbaceous species as a whole more similar to woody species. Across a wide range of habitats in the Netherlands, leaf P was higher in forbs and grasses than shrubs and trees, but leaf N showed less variability between growth forms (Ordoñez et al. 2010). Wright et al. (2005) determined that variation in leaf N and P is small between growth forms across diverse habitats worldwide and cautioned against generalizing this relationship at larger ecological scales. Taken with previously published analyses, my study supports the Wright et al. (2005) hypothesis that leaf nutrient allocation patterns are site dependent and not easily scaled up to broader contexts.

Compared to forbs, graminoids had greater levels of C relative to the macronutrients in my study. Graminoids were indistinguishable from forb and woody leaf C and N concentrations. Graminoid foliar N levels were similar to forbs and woody plants of an Italian mire (Bombonato et al. 2010) and across habitats in the Netherlands (Ordoñez et al. 2010), but not habitats of China (Han et al. 2011). In the HMFC community, graminoids also contained higher amounts of P and K relative to Ca and Mg than forb and woody species. Similar to the findings of my study, graminoids had the lowest foliar Ca and Mg and moderate K in other plant communities (Bombonato et al. 2010, Han et al. 2011). Foliar P was more variable between growth forms of different plant communities. In the HMFC community, leaf P of graminoids was similar to forbs, but greater than that of woody species. This finding is comparable with plants across habitats in the Netherlands (Ordoñez et al. 2010). In contrast, graminoid foliar P was among the lowest compared to other growth forms in an Alpine mire (Bombonato et al.

2010) and broad habitat types across China (Han et al. 2011). Substrate age may factor in to these differences, as P is gradually leached away from older soils (Epstein 1972), and is more limiting to plant growth than K, Mg, or Ca (Chapin 1980). Across systems, graminoids appear to be more variable in leaf P allocation than forbs and woody plants.

Generally, woody species had lower levels of leaf macronutrients than forbs; however, leaf Ca was similar between woody and forb species. This contrasts with Han et al. (2011), who found that not only Ca, but N, P, and Mg, of some woody species were as high as or higher than forbs. That study further categorized woody species as deciduous or evergreen and broadleaf or coniferous. This more detailed separation of woody growth forms helps explain the difference in results from my study, where the woody species are almost entirely deciduous. Variability across that study system, which was comprised of broad habitat types in China with marked shifts in plant strategy, was also greater than in the HMFC community.

Another way to assess leaf nutrient strategies is by examining patterning among nutrients. Fewer leaf nutrients were correlated in woody plants than forbs in my study, suggesting a weaker set of tradeoffs in woody species. Strong correlations among foliar nutrients were also found among a mostly herbaceous flora in central England (Thompson et al. 1997). Fewer correlations were observed in forbs and graminoids of Western European forests, with graminoids exhibiting even weaker correlations among leaf nutrients than forbs (Meerts 1997). Compared to my study, leaf nutrients in a broad range of tropical tree species had stronger patterns of correlation (Masunaga et al. 1998). Soil fertility tends to be lower in tropical rain forests than temperate forests (Harris 1974), so plants may have stronger leaf nutrient correlations in low-nutrient

environments. While the associations of C, N, and to a lesser extent P, are documented in the literature (e.g., Sterner and Elser 2002), additional studies are warranted to understand the meaning of plant nutrient associations between other leaf nutrients, as much less is known about these relationships (Ågren 2008, but see Ågren and Weih 2012). Strong correlations among forbs of the HMFC suggest this growth form has a more unified suite of growth strategies, whereas there may be more variation among woody plant growth strategies or no dominant growth strategy, due to greater allocation to structure than other leaf metabolic processes.

#### *Origin and leaf nutrients*

When analyses ignored variation in growth form, native plants had higher C and lower K levels compared to exotic plants. While this difference is important to consider, distinguishing plants by growth form is necessary to avoid confounding results. Leaf nutrient allocation did not differ by origin after growth form was taken into account. Native and exotic species within the HMFC community have already been shown to have similar population dynamics based on frequency and cover metrics (Meiners 2007, Meiners et al. 2009). Despite having evolved in separate ecological communities, exotic species acquire levels of foliar nutrients similar to equivalent native species in this community. This similarity further substantiates the hypothesis that native and exotic species are not functionally different and that variance among species is instead related to plant invasion potential (Thompson et al. 1995). Regardless of origin, particular traits define a successful plant, and these traits tend to be adapted to the nutrient-rich and disturbed habitats prevalent in modern environments (Thompson and Davis 2011).

At the community level, differences between native and exotic species were minimal. In an Australian riparian community, while extinct native species' functional traits differed from the exotic species, native species that persist have similar functional traits to exotic species that co-occur (Kyle and Leishman 2009). Traits that are best suited to plant survival within a community are comparable between native and exotic species. Native and non-native species have been found to be functionally similar within habitat types, but different when compared at a broader scale of alpine habitats (Dainese and Bragazza 2012). Resource allocation strategies differ among growth forms but vary less by origin.

Leaf nutrients of growth forms in the HMFC community did not vary by origin, but other communities have shown variation by origin. Native herbaceous plants had significantly lower N, P, and K in their shoots (leaves and stems) than exotic herbaceous species in Southwestern Australia (Foulds 1993). Daneshgar et al. (2013) found native forbs and C<sub>3</sub> grasses to have higher C:N than their exotic counterparts, while C:N was similar between native and exotic C<sub>4</sub> grasses. Among forest trees of Bangladesh, foliar N and K were significantly lower in native than exotic species (Osman and Sikder 2000). Further distinction by species' invasive potential is warranted to understand the variations in plant growth strategies.

#### *Invasiveness and leaf nutrients*

Invasive plants are those that rapidly expand their distribution within a given geographic range. A plant's invasive potential is separate and unique from its place of origin. Few studies have compared leaf nutrient differences between invasive and non-

invasive plants, regardless of origin. More often, the differences in leaf nutrients between exotic invasive and native plants have been compared (e.g., Leishman et al. 2007; Peñuelas et al. 2010). Exotic invasives have leaf traits associated with faster growth than natives (Sharma and Dakshini 1998, Leishman et al. 2007), although C capture has been shown to be similar between these groups (Leishman et al. 2010). Exotic invasives, compared to their native congeners, had faster root turnover, which was associated with higher N uptake and faster growth capacity (Smith et al. 2014). In addition to superior growth related to aboveground-belowground interactions, exotic invasive plants tend to be more resource efficient than natives in photosynthetic efficiency and leaf nutrient allocation (Sharma and Dakshini 1998, Godoy et al. 2011, Heberling and Fridley 2013). Comparisons of invasive and native species do not necessarily take into account the invasion potential of the natives, however. Following the recommendation of van Kleunen et al. (2010a), my study assessed leaf nutrient differences between invasive and non-invasive plants, regardless of origin.

In the community-wide analysis presented here, invasive plants did not have different leaf nutrient levels than non-invasive plants, and this relationship did not change after accounting for growth form. Larger scale analyses such as the current study are not frequently available in the literature. Of studies looking at differences between invasive and non-invasive plants, most compare traits between small suites of species. In one such analysis, leaf N of invasive and non-invasive pine species was not significantly different (Matzek 2011). Another study found invasive species to have significantly lower leaf N than their non-invasive congeners (Feng et al. 2008). While greater leaf nutrient concentration may be beneficial to the establishment of some invasive species, it is not a

universal predictor of invasive species success within a community. Rather than looking at leaf nutrients alone, comparing the suite of traits that represent fast growth and other means of establishment success (e.g., dispersal), as well as considering environmental conditions of the site, may be necessary to distinguish differences between invasive and non-invasive species (Pyšek and Richardson 2007, Leishman et al. 2007, 2010).

A number of leaf functional traits, including SLA, indicate that invasive species may have greater performance than non-invasive species, given suitable environmental conditions (Burns 2006, Grotkopp and Rejmánek 2007, Feng et al. 2008, Matzek 2011), but this is not a universal finding (van Kleunen et al. 2011). Feng et al. (2008) speculated that invasive species allocate more N to photosynthesis and less to cell walls, which accounts for the greater SLA, and may contribute to higher photosynthetic N use efficiency. Under high resource conditions, invasive species invested in new leaves (higher leaf area ratio) rather than increasing leaf N, perhaps to improve photosynthetic capacity (Godoy et al. 2011).

SLA was significantly higher in non-invasive forbs of the HMFC (mean SLA of non-invasive forbs =  $338.57 \text{ cm}^2/\text{g}$ ; invasive forbs =  $204.32 \text{ cm}^2/\text{g}$ ), but there was no difference between non-invasive and invasive woody species (mean SLA of non-invasive woody species =  $161.83 \text{ cm}^2/\text{g}$ ; invasive woody species =  $197.74 \text{ cm}^2/\text{g}$ ). Invasive woody seedlings may have higher SLA than non-invasive woody seedlings (Grotkopp et al. 2002, Grotkopp and Rejmánek 2007), but SLA as a successful invasion strategy may only be useful in early stages of invasion (Theoharides and Dukes 2007). In the HMFC community, having a higher SLA appears not to be a strategy used by invasive species to outcompete non-invasive species.

In my study, there was a high degree of overlap between native and non-invasive plant species and between exotic and invasive species. That is, species that were native often were non-invasive, and species that were exotic often were invasive, which makes it difficult to draw conclusions based on origin or invasiveness classification alone. It would be interesting to compare pools of species from each of these groups where there is minimal overlap, to investigate these relationships and discover what patterns emerge.

#### *Leaf-height-seed scheme and leaf nutrients*

In an attempt to create a simplified plant ecology strategy scheme that also captured meaningful variation in plant traits and could be compared across plant studies globally, Westoby (1998) proposed a leaf-height-seed (LHS) scheme. The central traits of this scheme – SLA, maximum height, and seed mass – are easily quantifiable and are correlated with plant metrics that are more challenging to measure. SLA indirectly measures photosynthesis and growth rate; maximum height indirectly describes plant structure and allocation strategies; seed mass foretells the chance of successful dispersal and opportunity for establishment. Westoby created an unsophisticated scheme intending for it to be applied broadly, even by researchers who were not directly interested in using SLA, height, or seed mass data. Westoby’s LHS article has been cited hundreds of times and used in several studies (e.g., Lavergne et al. 2003; Golodets et al. 2009; Laughlin et al. 2010; De Frenne et al. 2011; Jia et al. 2011; Pollock et al. 2012). My study analyzed the relationship between leaf nutrients and the LHS scheme to provide a linkage to a broader plant strategy.

A measure of metabolic activity, SLA was correlated only with leaf nutrients within forbs, with a positive correlation between leaf N and SLA ( $r = 0.39168$ ,  $p = 0.0011$ ). This result aligns with a global survey that found leaf N correlates positively with SLA across a large suite of woody and herbaceous plants (Reich et al. 1997). Leaf N has also been shown to correlate with SLA across species in a pine forest dominated by forbs (Laughlin et al. 2010). The lack of a correlation of leaf nutrients with SLA in woody plants in the HMFC community contrasts with findings that show leaf N of woody species is positively correlated with SLA (Hoffmann et al. 2005, Domínguez et al. 2012). Additional nutrients that correlate with SLA in woody plants vary in other studies. Among savanna and forest trees, P and K but not Ca and Mg were correlated positively with SLA (Hoffmann et al. 2005). In a mixed oak forest community, leaf Ca and Mg but not P and K were positively correlated with SLA among trees (Domínguez et al. 2012). The relationship between SLA and leaf nutrients appears to be site-specific, perhaps linked to soil nutrient and water availability within a community (Douma et al. 2012).

Seed mass of forbs and woody species was correlated with individual leaf nutrient concentrations, particularly leaf N (forbs only,  $r = 0.44628$ ,  $p = 0.0006$ ) and Mg (positively for forbs,  $r = 0.48435$ ,  $p = 0.0002$ ; negatively for woody species,  $r = -0.46707$ ,  $p = 0.0047$ ), while in graminoids it was not related (in a sample of only 13 species). These results are similar to a mostly forb community in a semi-arid pine forest, in which seed mass was positively correlated with leaf N (Laughlin et al. 2010). In contrast, seed mass was not correlated with leaf N among herbaceous plants (forbs and graminoids) across habitats of varying elevation in Europe (Pierce et al. 2014). Separating forbs from graminoids might clarify the relationship between seed mass and leaf nutrients of each

growth form since the leaf nutrient profile of graminoids may be quite different from forbs. Although more analysis is warranted before drawing conclusions about the relationship between these plant traits, it appears that leaf nutrients are a poor predictor of seed mass. It may be hypothesized that the rapid growth strategy associated with greater leaf nutrient levels in forbs might also be correlated with low seed mass. Similarly, slow-growing woody species that have lower levels of leaf nutrients might be correlated with greater seed mass. However, the wide variability in seed mass among both forbs and woody plants suggests that any relationship between leaf nutrients and seed mass is indirect.

Plant height at maturity and leaf nutrients were not correlated within any growth form. This supports earlier findings that height of herbaceous plants was not correlated with leaf C or N (Pierce et al. 2014), and that leaf N and P were mostly not different among species of various statures in a tropical rain forest (Bigelow 1993). The lack of association is perhaps not surprising as plant height is a light acquisition strategy (Tilman 1988) and would largely be driven by carbon allocation in stems. Light availability, along with soil fertility and hydraulic pressure, contributes to plant height (Givnish 1982, Koch et al. 2004, Cramer 2012), and leaf nutrients appear not to be an indicator for this trait.

Separating plant species into growth forms was critical, as the marked differences among groups in traits generated spurious correlations. If species were not separated by growth form, correlations between each of the functional traits and leaf nutrients were significant. Because forb, graminoid, and woody species have unique leaf nutrient acquisition patterns, as determined in my study and by others (e.g., Bombonato et al.

2010; Han et al. 2011), growth form should be accounted for before comparing other plant functional traits.

### *Succession and leaf nutrients*

Without first distinguishing plants by growth form, leaf nutrients were correlated with succession. However, peak year in succession was not correlated with leaf nutrient levels within plant growth forms of my study. Leaf nutrient acquisition varies by soil fertility, site history, and environmental conditions; successional age of the community factors in to each of these components (Tilman 1988, Walker and Wardle 2014). When soil nutrients are not limiting, plants have a faster rate of growth and more rapid turnover, especially early in succession when light and nutrient resources are high (Tilman 1987). In intermediate stages of succession soil fertility may increase, in part due to the turnover of early successional species and the establishment of N-fixing plants (Vitousek and Reiners 1975, Knops and Tilman 2000), although legumes were not prevalent in the HMFC community.

Communities not yet in advanced stages of succession may exhibit no change in leaf nutrient acquisition over time (Reich et al. 1995, Zhang et al. 2013), while late successional communities may have diminishing leaf nutrients (Vitousek et al. 1995, Parfitt et al. 2005). Soils may remain relatively nutrient rich in mid stages of succession due to the nutrient cycling that occurs with a more rapid turnover of the early and intermediate successional herbaceous species. As time progresses and the rate of plant turnover slows, N and P become decreasingly available in the soil and plants become increasingly efficient in nutrient use (Kazakou et al. 2007). In some plant communities,

leaf nutrients decline within shorter periods of time (Gleeson and Tilman 1990, Poorter et al. 2004, Kazakou et al. 2007), which may be attributable to soils already depleted in nutrients (e.g., Gleeson and Tilman 1990). While leaf N and P are growth-limiting nutrients and may not change significantly over long periods of time, leaf K, Ca, and Mg have been shown to decrease with soil age (Reich et al. 1995, Vitousek et al. 1995). In nutrient-depleted soils, leaf nutrient levels may not change over time (Navas et al. 2010), and nitrogen may remain a limiting nutrient regardless of plant community age (Chai et al. 2015).

With 53 years of development after agricultural use of the land was discontinued, the HMFC plant community is likely still in the middle stages of succession. These plants may show signs of leaf nutrient depletion as the community progresses into more advanced stages of succession. Woodwell et al. (1975) found that in a late-successional oak-pine forest of New England, nutrient concentration in plant tissues was highest early in succession among the dominant forbs and small shrubs, transitioning to lower nutrient concentrations in plant tissues from shrubs to early emerging trees in later stages of succession, and ending in intermediate nutrient concentrations of late succession and slow growing trees. In the HMFC community, there is a significant correlation between leaf nutrients and peak successional year across all growth forms (PCA Factor 1  $r = -0.29866$ ,  $p = 0.0008$ ; PCA Factor 2  $r = 0.23611$ ,  $p = 0.0088$ ). By growth form, however, there is no correlation. This suggests that the pattern of change over a successional gradient is one of progression in dominance by growth form rather than a change in leaf nutrient allocation across all species within the community.

Understanding the role of leaf nutrients in plants of varying growth form, origin,

and invasiveness across a successional gradient will inform restoration efforts of communities such as those affected by plowing. Changes to the structure and composition of a plant community over time alter nutrient cycles and the availability of essential elements to plant growth (Chapin et al. 2011). Through restoration efforts, a plant community may reach a state of dynamic equilibrium, with a heterogeneous mixture of species reflecting a stable and resilient population (Shackelford et al. 2013). An awareness of leaf nutrient variability across species will facilitate the process of community restoration by identifying the functional characteristics of species that represent the desired successional stage.

## Conclusions

Plants use leaf nutrients to conduct metabolic processes essential for growth, reproduction, and maintenance (survival). While C and N are needed in large quantities and are therefore often included in plant analyses, minerals P, K, Mg, and Ca are also essential to plant health but are less commonly investigated. Studying a full suite of nutrients conveys subtleties in plant resource allocation by more directly analyzing the linkage with metabolic processes rather than relying on surrogate functional traits such as SLA, height, or seed mass. By looking at traits that directly influence plant processes, complex pathways that allow for plant success, such as invasiveness, may be better understood.

The nuances of leaf nutrient patterning do not translate well across ecological scales. At the community level, my study shows that variation among growth forms contributes to leaf nutrient allocation patterns. This finding contrasts with the weak relationship between leaf nutrients and growth form at the global scale (Wright et al. 2004, 2005). To understand plant strategies in leaf nutrient use within a community, distinguishing between growth forms is necessary. When this is done, differences in leaf nutrient allocation by origin, invasiveness, and successional dominance are minimal relative to the range across species, such as occurred in the HMFC plant community.

Compared to single-nutrient studies, multi-trait comparisons of leaf nutrients are more powerful in describing subtle variations in plant allocation strategies. Leaf nutrients provide a more direct mechanistic link to local leaf metabolism than SLA, height, or seed mass. For this reason, leaf nutrient data should be incorporated with other plant functional traits for a better understanding of leaf economic strategies in the full context

of plant life history patterns. This awareness will inform restoration efforts of plant communities undergoing succession from a disturbance event such as plowing.

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**Appendix.** List of species used in the study.

<b>Species</b>	<b>Family</b>	<b>Form</b>	<b>Origin</b>	<b>Invasiveness</b>
<i>Abutilon theophrasti</i>	Malvaceae	forb	exotic	invasive
<i>Acalypha rhomboidea</i>	Euphorbiaceae	forb	native	non-invasive
<i>Acer negundo</i>	Sapindaceae	woody	native	invasive
<i>Acer platanoides</i>	Sapindaceae	woody	exotic	invasive
<i>Acer rubrum</i>	Sapindaceae	woody	native	non-invasive
<i>Achillea millefolium</i>	Asteraceae	forb	native	non-invasive
<i>Ageratina altissima</i> var. <i>altissima</i>	Asteraceae	forb	native	non-invasive
<i>Agrostis stolonifera</i>	Poaceae	graminoid	exotic	non-invasive
<i>Ailanthus altissima</i>	Simaroubaceae	woody	exotic	invasive
<i>Alliaria petiolata</i>	Brassicaceae	forb	exotic	invasive
<i>Ambrosia artemisiifolia</i>	Asteraceae	forb	native	invasive
<i>Apocynum cannabinum</i>	Apocynaceae	forb	native	non-invasive
<i>Asclepias syriaca</i>	Apocynaceae	forb	native	invasive
<i>Asplenium platyneuron</i>	Aspleniaceae	forb	native	non-invasive
<i>Barbarea vulgaris</i>	Brassicaceae	forb	exotic	non-invasive
<i>Bromus racemosus</i>	Poaceae	graminoid	exotic	invasive
<i>Calystegia sepium</i>	Convolvulaceae	forb	native	non-invasive
<i>Carex</i> sp.	Cyperaceae	graminoid	n/a	n/a
<i>Carya</i> sp.	Juglandaceae	woody	native	non-invasive
<i>Celastrus orbiculatus</i>	Celastraceae	woody	exotic	invasive
<i>Centaurea transalpina</i>	Asteraceae	forb	native	non-invasive
<i>Chenopodium album</i>	Amaranthaceae	forb	exotic	invasive
<i>Circaea lutetiana</i>	Onagraceae	forb	native	non-invasive
<i>Cirsium arvense</i>	Asteraceae	forb	exotic	invasive
<i>Cirsium discolor</i>	Asteraceae	forb	native	non-invasive
<i>Conyza canadensis</i>	Asteraceae	forb	native	invasive
<i>Cornus amomum</i>	Cornaceae	woody	native	non-invasive
<i>Cornus florida</i>	Cornaceae	woody	native	non-invasive
<i>Cornus racemosa</i>	Cornaceae	woody	native	non-invasive
<i>Dactylis glomerata</i>	Poaceae	graminoid	exotic	non-invasive
<i>Danthonia spicata</i>	Poaceae	graminoid	native	non-invasive
<i>Daucus carota</i>	Apiaceae	forb	exotic	invasive
<i>Dianthus armeria</i>	Caryophyllaceae	forb	exotic	non-invasive
<i>Digitaria sanguinalis</i>	Poaceae	graminoid	exotic	invasive
<i>Elaeagnus angustifolia</i>	Elaeagnaceae	woody	exotic	invasive
<i>Elymus repens</i>	Poaceae	graminoid	exotic	invasive
<i>Erechtites hieracifolia</i>	Asteraceae	forb	native	non-invasive
<i>Erigeron annuus</i>	Asteraceae	forb	native	invasive
<i>Euthamia graminifolia</i>	Asteraceae	forb	native	non-invasive
<i>Fagus grandifolia</i>	Fagaceae	woody	native	non-invasive

<i>Fragaria virginiana</i>	Rosaceae	forb	native	non-invasive
<i>Fraxinus americana</i>	Oleaceae	woody	native	non-invasive
<i>Galium circaezans</i>	Rubiaceae	forb	native	non-invasive
<i>Geum canadense</i>	Rosaceae	forb	native	non-invasive
<i>Hackelia virginiana</i>	Boraginaceae	forb	native	non-invasive
<i>Hedeoma pulegioides</i>	Lamiaceae	forb	native	non-invasive
<i>Hedera helix</i>	Araliaceae	woody	exotic	invasive
<i>Hieracium caespitosum</i>	Asteraceae	forb	exotic	invasive
<i>Hieracium piloselloides</i>	Asteraceae	forb	native	non-invasive
<i>Impatiens capensis</i>	Balsaminaceae	forb	native	non-invasive
<i>Juglans nigra</i>	Juglandaceae	woody	native	non-invasive
<i>Juncus</i> sp.	Juncaceae	graminoid	n/a	n/a
<i>Juniperus virginiana</i>	Cupressaceae	woody	native	non-invasive
<i>Lactuca serriola</i>	Asteraceae	forb	exotic	non-invasive
<i>Leucanthemum vulgare</i>	Asteraceae	forb	exotic	invasive
<i>Ligustrum vulgare</i>	Oleaceae	woody	exotic	invasive
<i>Linaria vulgaris</i>	Plantaginaceae	forb	exotic	invasive
<i>Lindera benzoin</i>	Lauraceae	woody	native	non-invasive
<i>Lobelia inflata</i>	Campanulaceae	forb	native	non-invasive
<i>Lonicera japonica</i>	Caprifoliaceae	woody	exotic	invasive
<i>Lonicera maackii</i>	Caprifoliaceae	woody	exotic	invasive
<i>Lonicera tatarica</i>	Caprifoliaceae	woody	exotic	invasive
<i>Malus sylvestris</i>	Rosaceae	woody	exotic	non-invasive
<i>Microstegium vimineum</i>	Poaceae	graminoid	exotic	invasive
<i>Morus rubra</i>	Moraceae	woody	native	non-invasive
<i>Nyssa sylvatica</i>	Nyssaceae	woody	native	non-invasive
<i>Oenothera biennis</i>	Onagraceae	forb	native	invasive
<i>Parthenocissus quinquefolia</i>	Vitaceae	woody	native	invasive
<i>Penstemon hirsutus</i>	Plantaginaceae	forb	native	non-invasive
<i>Phalaris arundinacea</i>	Poaceae	graminoid	native	non-invasive
<i>Phleum pratense</i>	Poaceae	graminoid	exotic	non-invasive
<i>Phytolacca americana</i>	Phytolaccaceae	forb	native	invasive
<i>Pilea pumila</i>	Urticaceae	forb	native	non-invasive
<i>Plantago lanceolata</i>	Plantaginaceae	forb	exotic	invasive
<i>Polygonum persicaria</i>	Polygonaceae	forb	exotic	non-invasive
<i>Polygonum scandens</i>	Polygonaceae	forb	native	non-invasive
<i>Polygonum virginianum</i>	Polygonaceae	forb	native	non-invasive
<i>Portulaca oleracea</i>	Portulacaceae	forb	exotic	invasive
<i>Potentilla simplex</i>	Rosaceae	forb	native	non-invasive
<i>Prunella vulgaris</i>	Lamiaceae	forb	native	non-invasive
<i>Prunus avium</i>	Rosaceae	woody	exotic	non-invasive
<i>Prunus serotina</i>	Rosaceae	woody	native	invasive
<i>Quercus alba</i>	Fagaceae	woody	native	non-invasive

<i>Quercus coccinea</i>	Fagaceae	woody	native	non-invasive
<i>Quercus palustris</i>	Fagaceae	woody	native	non-invasive
<i>Quercus rubra</i>	Fagaceae	woody	native	invasive
<i>Quercus velutina</i>	Fagaceae	woody	native	non-invasive
<i>Rhus glabra</i>	Anacardiaceae	woody	native	non-invasive
<i>Rosa multiflora</i>	Rosaceae	woody	exotic	invasive
<i>Rubus allegheniensis</i>	Rosaceae	woody	native	non-invasive
<i>Rubus flagellaris</i>	Rosaceae	woody	native	non-invasive
<i>Rubus occidentalis</i>	Rosaceae	woody	native	non-invasive
<i>Rubus phoenicolasius</i>	Rosaceae	woody	exotic	invasive
<i>Rumex acetosella</i>	Polygonaceae	forb	exotic	invasive
<i>Rumex crispus</i>	Polygonaceae	forb	exotic	invasive
<i>Sanicula odorata</i>	Apiaceae	forb	native	non-invasive
<i>Sassafras albidum</i>	Lauraceae	woody	native	non-invasive
<i>Schizachyrium scoparium</i>	Poaceae	graminoid	native	non-invasive
<i>Setaria faberi</i>	Poaceae	graminoid	exotic	invasive
<i>Silene latifolia</i>	Caryophyllaceae	forb	exotic	invasive
<i>Solanum carolinense</i>	Solanaceae	forb	native	non-invasive
<i>Solidago canadensis</i>	Asteraceae	forb	native	invasive
<i>Solidago gigantea</i>	Asteraceae	forb	native	invasive
<i>Solidago juncea</i>	Asteraceae	forb	native	non-invasive
<i>Solidago nemoralis</i>	Asteraceae	forb	native	non-invasive
<i>Solidago rugosa</i>	Asteraceae	forb	native	non-invasive
<i>Symphotrichum ericoides</i> var. <i>ericoides</i>	Asteraceae	forb	native	non-invasive
<i>Symphotrichum lanceolatum</i> ssp. <i>lanceolatum</i> var. <i>lanceolatum</i>	Asteraceae	forb	native	invasive
<i>Symphotrichum pilosum</i> var. <i>pilosum</i>	Asteraceae	forb	native	non-invasive
<i>Taraxacum officinale</i>	Asteraceae	forb	exotic	non-invasive
<i>Toxicodendron radicans</i>	Anacardiaceae	woody	native	non-invasive
<i>Trifolium aureum</i>	Fabaceae	forb	exotic	non-invasive
<i>Trifolium pratense</i>	Fabaceae	forb	exotic	invasive
<i>Trifolium repens</i>	Fabaceae	forb	exotic	invasive
<i>Ulmus rubra</i>	Ulmaceae	woody	native	non-invasive
<i>Verbascum thapsus</i>	Scrophulariaceae	forb	exotic	invasive
<i>Verbena urticifolia</i>	Verbenaceae	forb	native	non-invasive
<i>Veronica officinalis</i>	Plantaginaceae	forb	exotic	non-invasive
<i>Viburnum dentatum</i>	Adoxaceae	woody	native	non-invasive
<i>Viburnum prunifolium</i>	Adoxaceae	woody	native	non-invasive
<i>Viola</i> sp.	Violaceae	forb	n/a	n/a
<i>Vitis</i> sp.	Vitaceae	woody	native	non-invasive